Chapter 9
Spinocerebellar and Cerebellospinal Pathways

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Abstract Although the cerebellum participates in many different functions, its coordinating role in learning and execution of movements remains its most visible aspect to our behavior. Multiple pathways convey information from the body to the cerebellum. These spinal pathways can be divided in systems that, either directly or indirectly, enter the cerebellar cortex to terminate as mossy fibers and in pathways that reach the cerebellum by way of the inferior olive and as a consequence will terminate as climbing fibers. Cerebellar processing is also mediated to the spinal cord by a multitude of routes. Corticospinal, rubrospinal, tectospinal, vestibulospinal and reticulospinal tracts may all, at least to some extent, be controlled by cerebellar output.

Keywords Cerebellar nuclei • Corticospinal tract • Rubrospinal tract • Reticulospinal tract • Spinocerebellar tracts • Spino-olivocerebellar tracts • Vestibulospinal tracts

Although it has become clear that the cerebellum is involved in many functions, its role in the control and coordination of reflexive as well as voluntary movements has been its most visible contribution to our behavior. In order to execute these tasks the cerebellum requires considerable input from the body by way of multiple spinocerebellar routes. Similarly, output of the cerebellum participating in the control of movements reaches its destination by several pathways. This chapter reviews the tracts that reach the cerebellum with information from the body as well as provide an overview of descending corridors used by the cerebellum to influence movements.

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9.1   Information Routes from Spinal Cord to the Cerebellum

Information from the body to the cerebellum should be divided into pathways that reach the cerebellum by way of the mossy fiber system and routes that reach the cerebellum by way of the inferior olive and its climbing fibers to the cerebellar Purkinje cells. In both pathways a distinction can be made into direct routes from spinal cord to cerebellum and inferior olive (Fig. 9.1a, b), respectively, or by way of pathways that use an intermediary in the (lower) brainstem.

9.1.1   Direct Spinocerebellar Mossy Fiber Tracts

Four direct tracts from the spinal cord that terminate as mossy fibers in the cerebellar cortex can be recognized. The column of Clarke (located medially in lamina VII at thoracic and upper lumbar levels, also called 'dorsal nucleus' or 'posterior thoracic nucleus'), is at the origin of the dorsal spinocerebellar tract. It ascends ipsilaterally in the superficial aspect of the dorsal half of the lateral funiculus and enters the cerebellum by way of the inferior cerebellar peduncle (Fig. 9.1a). It conveys mostly proprioceptive information from the ipsilateral lower body half. Stilling's nucleus, located medially within lamina VII at sacral levels and the central cervical nucleus are thought to be the tail and neck equivalent of the column of Clarke. However, in contrast to the dorsal spinocerebellar tract, fibers from Stilling's nucleus and the central cervical tract reach the cerebellum by way of a mostly contralateral route and by way of the superior cerebellar peduncle (Matsushita et al. 1995).

   The ventral spinocerebellar tract originates predominantly from the so-called spinal border cells within the lateral part of the ventral horn of the lumbosacral cord, and from cells located within the intermediate gray of the cervical enlargement. In addition, there are many cells scattered throughout the dorsal, intermediate and ventral parts of the entire cord that will send projections to the cerebellum. Most of these spinocerebellar fibers ascend by way of the contralateral ventral (or anterior) spinocerebellar tract (Kitamura and Yamada 1989), and enter the cerebellum along the superior cerebellar peduncle (Fig. 9.1a). Spinocerebellar neurons travelling by way of the ventral spinocerebellar tract convey information from wide receptive fields and are also targeted by descending supraspinal systems.

Fig. 9.1 (continued) its importance is doubted. The vestibulospinal tracts can be divided into the lateral vestibulospinal tract (*LVST*), originating from the lateral vestibular nucleus (*LV*) and whose cells are directly controlled by Purkinje cells of the lateral vermis, and the medial vestibulospinal tract (*MVST*) who is specifically controlled by M. The reticulospinal tracts (*RST*) can be divided into a medial tract, which originates from the pontine reticular formation and a more laterally positioned tract, which predominantly originates from the medullary reticular formation. For the sake of clarity the reticular tracts are only depicted on the contralateral side although they essentially are present bilaterally. Also note that the interstitiospinal tract is not depicted in this scheme. *Additional abbreviations*: *C* cuneate nucleus, *CC* column of Clarke, *CCN* central cervical nucleus, *G* gracile nucleus, *SB* spinal border cells, *SN* Stilling's nucleus
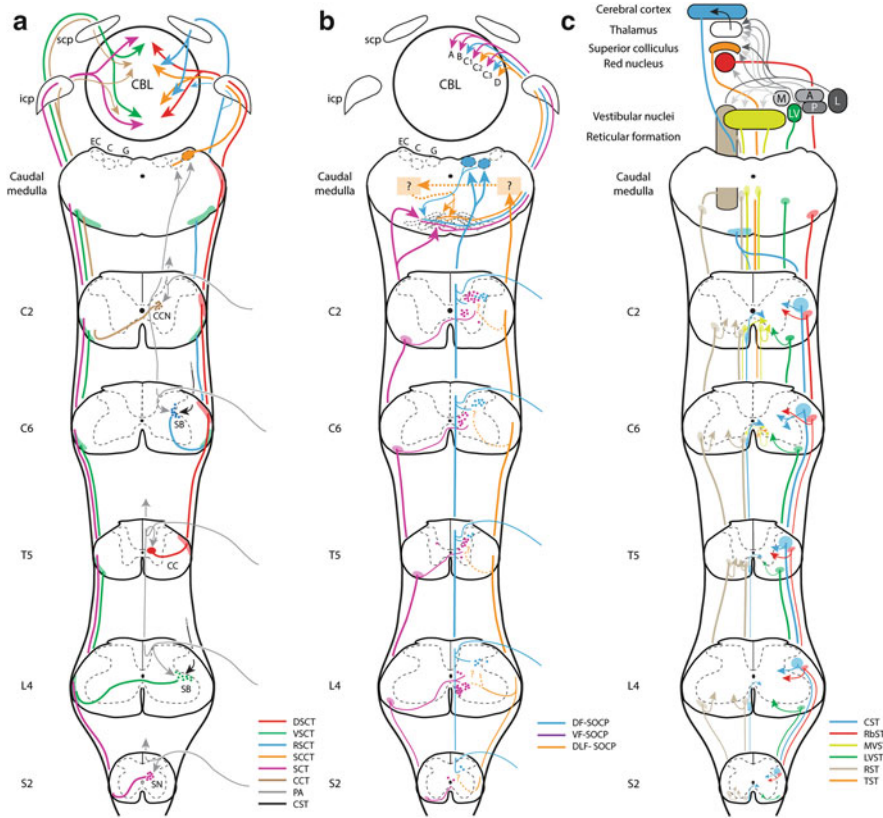
Fig. 9.1 Schematic diagrams showing the main ascending pathways from the spinal cord to the cerebellum (*CBL*) and the cerebellar influence on descending spinal tracts

(**a**) The direct spinocerebellar tracts. These tracts involve the dorsal spinocerebellar tract (*DSCT*), the ventral spinocerebellar tract (*VSCT*), the rostral spinocerebellar tract (*RSCT*), the sacral spinocerebellar tract (*SSCT*) and the cervicocerebellar tract (*CCT*). Due to the homology with the DSCT the external cuneocerebellar tract (*ECCT*) is also included in the direct spinocerebellar tracts. Note that some tracts take a contralateral course to the cerebellum but mainly terminate ipsilateral to their origin. Fibers mostly use the inferior cerebellar peduncle (*icp*), but some tracts enter the cerebellum by way of the superior cerebellar peduncle (*scp*)

(**b**) Essentially three spino-olivocerebellar paths (*SOCP*s) are recognized, although some paths can be further subdivided. A direct route from spinal cells to the inferior olive essentially takes a route by way of the contralateral ventral funiculus (*VF-SCOP*). A second route courses the ipsilateral dorsal funiculus (*DF-SCOP*), synapses at the dorsal column nuclei from where the contralateral inferior olive is targeted. This path, at least partly, originates from so called postsynaptic dorsal funiculus interneurons located in the dorsal horn. The third spinocerebellar path follows the ipsilateral dorsolateral funiculus (*DLF-SCOP*) and has one or two synaptic stations of unknown location before reaching the inferior olive. Single cerebellar cortical zones can receive input from multiple SOCPs

(**c**) Descending pathways influenced by cerebellar output. The corticospinal tract (*SCT*) is influenced by all cerebellar nuclei as these all reach the motor thalamus. The tectospinal tract (*TST*) can be influenced by the medial (*M*), posterior interposed (*P*) and lateral (*L*) cerebellar nuclei. It descends mostly contralateral to cervical levels. The rubrospinal tract (*RbST*) is activated by the-anterior interposed (*A*) nucleus. It descends in the lateral funiculus throughout the cord. In human

Although the spino-cuneo-cerebellar pathway involves a brainstem nucleus it can be considered the forelimb homologue of the dorsal spinocerebellar tract. The main intermediary is formed by the external cuneate nucleus which receives mostly proprioceptive input from forelimb primary afferents travelling within the dorsal funiculus. It enters the cerebellum by way of the ipsilateral inferior cerebellar peduncle terminating mostly unilaterally in the cortex of the spinocerebellum.

The rostral spinocerebellar tract is considered to be the forelimb equivalent of the ventral spinocerebellar tract. It mostly arises from neurons at the intermediate laminae of the cord throughout the cervical levels but, contrasting its lower limb homolog, their axons reach the cerebellum by way of an ipsilateral route passing through the ventral part of the lateral funiculus and entering the cerebellum by either the inferior or superior peduncles (Fig. 9.1a).

9.1.2   Indirect Spinocerebellar Mossy Fiber Tracts

The lateral reticular nucleus, situated ventrolaterally in the caudal medulla, is an important intermediary supplying spinal information to the cerebellum. It can be divided into a magnocellular dorsomedial, a parvocellular ventrolateral, and a sub-trigeminal part. In cat, physiological studies, often corroborated by tracing studies, have shown that the ventrolateral part mediates information from both lower limbs by way of the ventral flexor reflex tract, while the dorsomedial part receives proprioceptive information from the ipsilateral forelimb specifically (Pivetta et al. 2014; Azim et al. 2014).

The vestibular nuclei may also function as a brainstem intermediary transmitting spinocerebellar information as the central cervical nucleus also supplies afferents to predominantly the magnocellular part of the medial vestibular nucleus. This information may be involved in the control of the vestibulocollicular reflex (Matsushita et al. 1995). Similar to the vestibulo-ocular reflexes the vestibulocerebellum is likely to be involved in the adaptive control this reflex (Barmack 2003).

9.1.3   Cerebellar Targets of Spinocerebellar Mossy Fiber Tracts

Within the cerebellum, both the direct and indirect spinocerebellar mossy fiber projections are supplied bilaterally with an ipsilateral preponderance which indicates that the contralaterally ascending fibers recross in the cerebellum (Matsushita and Yaginuma 1989). Spinocerebellar mossy fibers mainly terminate in the so-called spinocerebellum, which mostly consists of the vermal and paravermal regions of the anterior lobe (and adjacent simple lobule) as well as in vermal and paravermal parts of lobule VIII and adjacent parts of VII and IX. A coarse somatotopy can be recognized in that the hindlimb is represented anterior to the forelimb in the rostral cerebellar lobules but posterior to it in its caudal representation. It is not known to what extent terminal clusters from axons travelling by way of the dorsal

spinocerebellar tract overlap with those from the ventral spinocerebellar tract. Spinocerebellar systems collateralize to the cerebellar nuclei but from the external cuneate nucleus these projections are sparse (Quy et al. 2011).

9.1.4 Spino-Olivocerebellar Pathways

Spino-olivocerebellar pathways (SOCPs) have been extensively studied in cat using electrophysiological techniques employing selective lesions of the spinal white matter (Oscarsson and Sjolund 1977). As such it was established that spinal afferents can affect olivary processing by way of the ventral (or ventrolateral), (dorso-) lateral, and dorsal funiculi (Fig. 9.1b).

The ventral funiculus SOCP originates from several clusters of neurons located at the deeper layers of the contralateral cord and includes the lateral cervical nucleus. These neurons relay mostly proprioceptive, but also cutaneous, information which, after crossing at segmental level ascends just ventral to the ventral spinocerebellar tract to reach the caudal part of contralateral medial accessory and entire dorsal accessory olive. Olivocerebellar axons from the caudal parts of the accessory olives again cross the midline to reach the cerebellum by way of the inferior cerebellar peduncle to terminate unilaterally in A and B zones of the vermis (caudal parts of medial and dorsal accessory olives, respectively), whereas the rostral dorsal accessory olive targets the paravermal C1 and C3 zones.

A second pathway from the spinal cord to the inferior olive uses the dorsal funiculus and relays at the dorsal column nuclei (DFSOCP). At least part of this pathway originates from neurons from the deeper layers of the dorsal horn and is also referred to as the postsynaptic dorsal column pathway to the inferior olive. Available evidence suggests that the postsynaptic dorsal column pathway originates from different spinal sources and mediates less sensitive and/or nociceptive signals to the inferior olive as compared to the direct spino-olivary route (Flavell et al. 2014).

Finally, the third spino-olivocerebellar route passes mostly through the ipsilateral lateral funiculus and relays through several, as yet not further specified, brainstem intermediaries before activating the contralateral inferior olive (i.e. rostral part of the medial accessory and the principal olives) that supply climbing fibers to the C2 and D zones.

SOCPs can activate climbing fibers of all major cerebellar zones (excepting those of the vestibulocerebellum) but do so with different latencies.

9.2 Information Routes from the Cerebellum to the Spinal Cord

Descending pathways to the spinal cord usually influence motor programming. However, obviously, several autonomic and visceral pathways are also directed to their respective spinal control sites. Here, we will concentrate on the first group of

descending routes in order to provide an overview of the involvement of the cerebellar control on these generally motor control pathways.

Classically, medial descending systems, which course through the ventral funiculus, and lateral descending systems, which pass the lateral funiculus, were distinguished by Lawrence and Kuypers (1968). Medial systems comprise the uncrossed medial corticospinal tract and the tectospinal, vestibulospinal, reticulospinal and interstitiospinal pathways. The lateral systems involve the crossed corticospinal tract and the rubrospinal tract (Ruigrok 2013).

9.2.1 Lateral Systems

The crossed corticospinal tracts originates mostly from the primary motor (area 4), premotor (area 6) and, to a lesser extent, from somatosensory (areas 1–3) cortices. As output from all cerebellar nuclei will reach the ventral lateral and ventral anterior parts of the thalamus (i.e. the classic 'motor' thalamus), but not the ventral posterior nucleus, cerebellar processing will be important for voluntary movement control (Fig. 9.1c). It should be noted that cerebellar control over the corticospinal tract originates from larger areas of the cerebellar cortex than the classic spinocerebellar regions. Presently, it is debated to what extent cerebellar output is involved in corticospinal information processing within somatosensory cortical regions (cf. Proville et al. 2014).

The rubrospinal tract originates from the magnocellular part of the red nucleus, which is under the exclusive cerebellar control of the anterior interposed nucleus (Fig. 9.1). Its fibers cross at the level of the nucleus and descend in the ventrolateral medulla to take up position in the lateral funiculus just ventral to, and partly intermingled with, the fibers from the crossed corticospinal tract. Although in most mammals the tract terminates throughout the spinal cord, its contribution to cervical processing seems to have increased in animals with reaching capacities of their forelimbs. In primates the importance of the rubrospinal tract seems to have degraded; in man only a few hundred rubrospinal fibers are described that may not even reach caudal cervical levels (Onodera and Hicks 2009).

9.2.2 Medial Systems

The origin of the uncrossed corticospinal tract seems to be similar to that of the crossed corticospinal tract. However, caudal to the pyramidal decussation it takes an ipsilateral route through the ventral funiculus to terminate predominantly contralaterally on interneurons in the medial part of the ventral horn.

The tectospinal tract originates from large cells in the deeper layers of the caudolateral part of the superior colliculus. As this structure is involved in directing gaze to objects of interest, this tract is involved in controlling head and neck position

relative to the body. Its fibers mostly decussate in the dorsal tegmental tract and descend in the ventral funiculus down to the upper cervical cord. Tectospinal projections are widespread and usually involve a segmental relay. Tecto-reticulo-spinal projections can also contribute to tectal control of spinal motor systems. Cerebellar output from the fastigial, posterior interposed and lateral cerebellar nucleus reaches the superior colliculus (Fig. 9.1c). As such these regions might influence tectospinal processing.

The vestibular nuclear complex, classically divided into a medial, spinal, lateral and a superior vestibular nucleus, is intimately connected with the cerebellum. Not only is a large part of its output directed to the cerebellar cortex and nuclei, but it also receives a main input from the cerebellum. Indeed, the vestibular complex is special because it is the only brainstem system that receives afferents from the cerebellar nuclei as well as directly from the cerebellar cortex. Descending output of the vestibular nuclei is directed the spinal cord by way of the medial and lateral vestibulospinal tracts (Fig. 9.1c). The medial tract descends by way of the medial longitudinal fascicle, entering and coursing the ventral funiculus at its dorsal aspects. Its fibers originate from the ipsilaterally located inhibitory neurons and from excitatory, but contralaterally located vestibular neurons. The medial tract terminates bilaterally in the ventromedial aspects of the spinal gray where they mostly influence motoneurons that innervate neck and axial musculature. It does not seem to descend beyond midthoracic levels. Vestibular neurons contributing to the medial vestibulospinal tract may receive information from either the medial cerebellar nucleus or from Purkinje cells of the vestibulocerebellum that project directly to the vestibular nuclei. The rostral part of the medial cerebellar nucleus provides a glycinergic projection to the ipsilateral medial vestibular nucleus and a glutamatergic projection to its contralateral counterpart (Bagnall et al. 2009).

The lateral vestibulospinal tract originates from the ipsilateral lateral vestibular nucleus (LV), is excitatory, and descends laterally in the ventral funiculus to terminate, throughout the length of the cord, in the ventromedial laminae of the spinal grey (Fig. 9.1c). Direct synaptic contacts with motoneurons that control extensor or anti-gravity muscles has been established (Arshavsky et al. 1986). Cerebellar control of the LV is provided by the axons of the Purkinje cells of the B-zone of the lateral vermis of the anterior lobe and lobule VIII. Indeed, as most LV neurons are active during the stance phase of locomotion, it was shown that cooling of the anterior cerebellar vermis results in prolonged stance phases (Arshavsky et al. 1986; Udo et al. 1976). Yet, using transneuronal labeling, it was demonstrated that B-zone Purkinje cells may influence both agonists and antagonists (Ruigrok et al. 2008).

The medioventral pontomedullary reticular formation forms the origin of several long descending systems that travel ipsilaterally in medial (mostly from pontine levels) and bilaterally in ventral or ventrolateral reticulospinal tracts (mostly from medullary levels: Fig. 9.1c). Many fibers provide collaterals to cervical as well as lumbar levels. Reticulospinal systems have been described as subserving many different functions as they are involved in maintaining and controlling ongoing motor activity of proximal but also distal muscles (e.g. Esposito et al. 2014), in the gating of somatosensory information to segmental as well as supraspinal levels, and in the

control of autonomic activity including pain modulatory systems (e.g. Fields 2004). Several regions of the cerebellar nuclei supply projections to the reticular formation and, as such, may influence processing in reticulospinal systems. The caudal part of the medial cerebellar nucleus projects contralaterally to the medial pontine reticular formation as well as to the dorsomedial medullary reticular formation. Other parts predominantly reach parvocellular reticular regions. The rostral part of the medial nucleus, although mostly supplying terminals to the vestibular nuclei, also projects to intermediate (mediolateral) levels of the reticular formation and to the lateral paragigantocellular nucleus. The medial cerebellar nucleus has also been implicated in the control of several autonomic functions (Nisimaru 2004). A second cerebellar nuclear area that is intercalated between the medial and the interposed nuclei has projections to selective regions of the contralateral pontomedullary reticular formation, such as the gigantocellular reticular nucleus. In rodents, a prominent ipsilateral projection emerges from the enlarged lateral part of the anterior interposed nucleus, termed the dorsolateral hump, and which supplies afferents to the parvicellular regions of the ipsilateral pontomedullary reticular formation but also invades the deeper layers of the spinal trigeminal nucleus. Stimulation evokes movements of lips, neck and forelimb (Cicirata et al. 1992). The dorsolateral hump receives its Purkinje fiber input from the D0 zone, which is intercalated between the D1 and D2 zones of lobules V–VII. It is not known if a primate equivalent exists. Finally, the connections of the lateral nucleus with the pontomedullary reticular formation are well documented for rat, cat and monkey and are particularly dense to the contralateral gigantocellular reticular nuclei (Fig. 9.1c). The projection originates mostly from the dorsal, magnocellular, aspects of the nucleus. Projections may also reach the ipsilateral reticular formation and have been shown to activate reticulospinal neurons monosynaptically (Tolbert et al. 1980). The role of this disynaptic dentate-reticulo-spinal connection is not yet clear.

The interstitiospinal tract originates from a region with scattered large neurons located within and surrounding the medial longitudinal fascicle at midbrain levels, and which is known as the interstitial nucleus of Cajal. This region is known to be involved in oculomotor control but at least some of its fibers descend ipsilaterally to the spinal cord where they terminate in laminae VII and VIII. The interstitiospinal tract has excitatory monosynaptic contacts with neck musculature but also provides di- and polysynaptic activations of other muscles (Fukushima et al. 1978; Holstege and Cowie 1989). Cerebellar projections to the interstitial nucleus of Cajal arise mostly from the medial cerebellar nucleus, but other areas also contribute.

9.3   Conclusion

The cerebellum is widely known as a structure with a uniform internal circuitry that processes information in a stereotypic way. Within the internal circuitry a number of sagittally organized modules are recognized which form functional entities (Apps and Hawkes 2009; Ruigrok 2011). The organization of the input to these modules

and the organization of their output channels, therefore, will determine the type of information processed within such a module and which structures will be informed of its result. The overview presented in this chapter demonstrates that detailed knowledge of the spino-cerebellar and cerebello-spinal connections with these modules is still not at a level that enables a deeper understanding of cerebellar functions. A detailed description of the interaction of the various spinocerebellar systems with the cerebellar modular circuitry is required together with an improved perception of how the output of modules is distributed to and processed within the centers from which descending tracts originate.

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